

VOLUNTARY CONTROL OF THE SHAPE OF THE INFLATED VOCAL SAC BY THE AUSTRALIAN LEPTODACTYLID FROG LIMNODYNASTES TASMANIENSIS

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Summary

Individuals of the Australian leptodactylid frog *Limnodynastes tasmaniensis* were observed to voluntarily modify the shape and position of the inflated vocal sac structure. A study of the anatomy of superficial mandibular features was correlated with profile sketches of the positions occupied by the inflated vocal sac structure. In the absence of audibly detectable differences in mating calls emitted from partially or completely inflated vocal sacs, it was concluded that neither shape nor position of the vocal sac structure influence call composition.

Introduction

The sounds produced by male frogs to advertise their territorial inclinations or sexual aspirations have been the subject of study by many workers. Recognition of the specificity of mating calls has resulted in numerous analyses of the calls, and of their role in pre-mating isolating mechanisms. In contrast, data on the actual mechanics of sound production, and particularly of the role of the inflated vocal sac are insufficient to substantiate some widely accepted assumptions.

It may be inferred from the behaviour of species lacking vocal sacs that such structures amplify sounds produced in the larynx. For example, Moore (1961) noted that such a species, *Litoria (Hyla) lesueuri*, had "a peculiar soft call that I found difficult to detect beyond ten feet". Whether the vocal sac contributes to detectable call parameters (spectral composition) is uncertain, although in *Rana catesbiana*, Capranica (1965) concluded that variation in capacity did not.

One would expect differences in the gross morphology of the sac, and particularly its shape and position in relation to the larynx, to influence call structure. Whether this is in fact the case remains uncertain.

In the course of studies on the morphology and function of anuran vocal sac structures, some individuals of the Australian leptodactylid frog *Limnodynastes tasmaniensis* were observed to be capable of voluntarily modifying both the shape and position of the inflated vocal sac structure. Comparable observations have not been reported on any other anuran species. The modification could be distinguished from partial inflation of the entire

structure, and indicated the existence of a refined mechanism of control of the muscles or skin underlying the vocal sac.

Detailed attention was therefore paid to *L. tasmaniensis* to establish the morphology of the submandibular region, the positions of submandibular structures during vocal sac distension, the mechanism by which changes in the shape and position of the inflated vocal sac structures are effected, and the influence of shape and position of the vocal sac structure on the emitted call.

Material and Methods

Over a period of several years observations were made on *Limnodynastes tasmaniensis* calling in static or very slowly running water, in the vicinity of Adelaide and the adjacent Mt. Lofty Ranges. Specimens in breeding condition were transferred to vivaria in the laboratory in early August 1969 where they continued to call during the daytime.

Profile drawings were prepared of specimens observed to exhibit the control of the vocal sac structure described in this paper. The same specimens were then killed in a 5% solution of urethane, fixed in 60% alcohol, and the position of the superficial mandibular muscles and of the vocal sac subsequently determined by dissection with the aid of a low-power binocular microscope.

"Vocal sac" is here used to refer to the inflatable diverticula intruding between the superficial ventral mandibular muscles, and the deeper musculature of the tongue and hyoid apparatus. The vocal sac together with the *Musculus intermandibularis*, *M. inter-*

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hyoideus and the skin ventral to these muscles are collectively referred to as the "vocal sac structure".

Morphology of the Vocal Sac Structure

A description of anuran vocal sac structure has been presented elsewhere (Tyler, 1971). The musculature of *L. tasmaniensis* is atypical in that the most anterior fibres of the intermandibularis do not follow the customary transverse path, but pass forwards and attach upon the ventral surface of the submentalis (Fig. 1) so obscuring much of the latter muscle from the ventral aspect. The most antero-medial segment of the intermandibularis is aponeurotic.

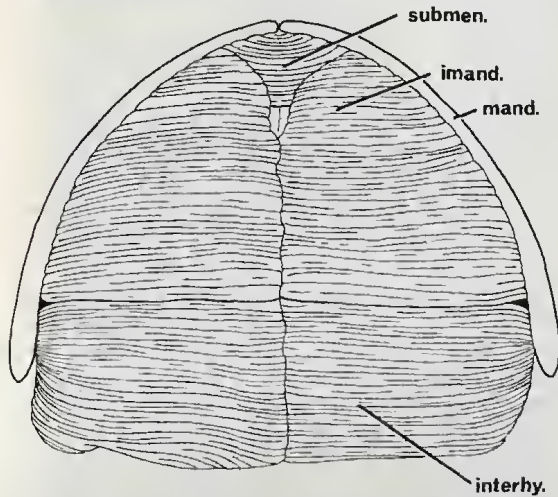


Fig. 1. Superficial mandibular musculature from ventral aspect. imand. = Musculus intermandibularis; interhy. = M. interhyoideus; mand. = Mandible; submen. = M. submentalis.

The only myo-integumental attachment in the submandibular region is via the post-mandibular septum.

The innervation of the superficial mandibular musculature corresponds to that described by de Watteville (1875) in *Rana esculenta*. The skin underlying the intermandibularis is innervated by the inframaxillary branch of the fifth cranial nerve, and the skin beneath the interhyoideus by the seventh.

The vocal sac extends antero-medially to the posterior border of the intermandibularis and antero-laterally to the limits of the elongate vocal sac apertures.

Calling Behaviour

Two races of this species are recognised on the basis of differences in mating call: a

southern call race characterised by "a short single pulsed mating call", and a northern call race characterised by "a mating call composed of two to five pulses" (Littlejohn and Martin, 1965; Littlejohn, 1967). The frogs which I studied are members of the northern call race.

Limnodynastes tasmaniensis usually calls from an exposed position in water. The frog floats with the body submerged and the limbs extended. Prior to inflation of the vocal sac the long axis of the body is horizontal.

Inflation of the vocal sac alters the buoyancy of the individual. The head and chest are raised so that the vocal sac structure lies above the level of the water. The longitudinal axis of the body is tilted to an angle of approximately sixty degrees from the horizontal, and the trunk submerges.

The mating call of this species is customarily emitted with the entire mandibular region grossly distended. In profile the vocal sac structure extends beyond the anterior portion of the sternum (Fig. 2A); when viewed from above the vocal sac structure extends laterally beyond the mandibles.

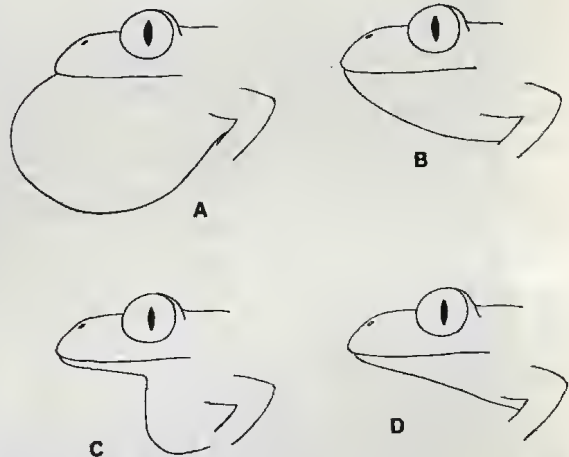


Fig. 2. Profile views of inflated vocal sac. A = fully inflated; B = partially deflated; C = posteriorly inflated; D = entirely deflated.

Following completion of vocal activity the vocal sac structure is usually rapidly and entirely deflated (Fig. 2D). On occasions however it is either partially but uniformly deflated (Fig. 2B), or the anterior portion of the structure is completely deflated whilst the posterior remains inflated (Fig. 2C). Intermittent vocal activity is occasionally resumed with the vocal sac structure thus incompletely

deflated. There was no audibly detectable difference between the calls emitted with the vocal sac maximally inflated or incompletely deflated.

Discussion

Studies on the disposition of submandibular vocal sacs in other anuran genera indicate that they occupy one of two positions: they extend anteriorly above the interhyoideus and intermandibularis, or lie above the interhyoideus but do not extend anteriorly beyond the border of the intermandibularis.

From the observation that when the vocal sac of *L. tasmaniensis* is maximally inflated the entire submandibular region is distended, this species could be anticipated to possess a vocal sac of the former type, with the intermandibularis composing the muscular lining of the anterior segment of the inflated vocal sac structure. The vocal sac is however of the latter type and so is not free to intrude above the intermandibularis. Vocal sac inflation cannot therefore direct any portion of this muscle into a position above the intermandibularis.

Although the hyoid plate lying above the intermandibularis can be considerably raised or depressed in freshly killed frogs, it is attached posteriorly via the postero-medial processes to the larynx, which is attached via other processes to the oesophagus, heart and lungs. Thus the hyoid may depress the intermandibularis, but the possibility of the former being also capable of forcing the latter against the anterior segment of the skin during maximal inflation can be excluded. It is therefore concluded that during maximal inflation the interhyoideus passes forwards to underly the intermandibularis (Fig. 3).

The anterior margin of the posteriorly inflated vocal sac structure correlates perfectly with the position of the border between the intermandibularis and interhyoideus, and indicates quite clearly that in this form of inflated structure the interhyoideus is by some means prevented from intruding beneath the intermandibularis. The profile view also reveals that the intermandibularis is not depressed. Thus the skin covering the intermandibularis appears to be responsible for restricting the inflated interhyoideus to a posterior position.

The term "elastic" has been applied to a submandibular skin which is recognised to contribute to the potential distension of the vocal sac structure (Inger, 1956; Blair, 1964). The extreme and prolonged distension of submandibular skin, such as occurs during vocal

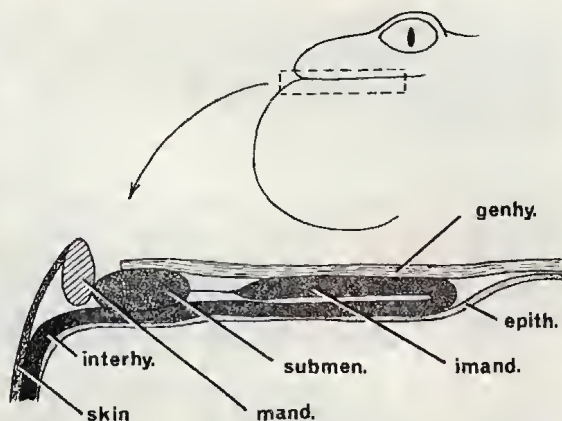


Fig. 3. Interpreted position of superficial mandibular muscles during maximal inflation of vocal sac structure. Enlargement represents sagittal section. epith. = epithelial lining of vocal sac; genhy. = *Musculus geniohyoideus*. For Key to other abbreviations see caption to Figure 1.

activity associated with the breeding season, stretches it and may result in loss of the ability to contract fully. The skin becomes irregularly pleated and hangs loosely in species that lack direct myo-integumental contact (e.g. many Neotropical *Hyla* spp.).

The tissue most likely to produce skin contraction is the thin layer of muscle at the base of the corium. In view of the difference in innervation of the skin beneath the intermandibularis from that beneath the interhyoideus, the existence of a nervously mediated mechanism for constricting one portion and not the other, so producing the effect observed in *L. tasmaniensis*, is indicated.

The absence of any audibly detectable difference between the calls of *L. tasmaniensis* emitted with the vocal sac completely or partially inflated, suggests that neither shape nor position in relation to the larynx influence spectral call composition.

Although the observations are subjective, the conclusion is supported by Blair's (1959) arrangement of anuran species into groups on the basis of similarities in mating-call structure, instead of the customary means of resemblance in internal or external morphology. Blair so divided thirteen species of *Hyla* occurring in the U.S.A. into several species groups. This resulted in associating the species *baudini* with the *H. versicolor* group, although he noted that whereas *versicolor* and the other species had a customary submandibular ("sub-gular") vocal sac structure, *baudini* possessed a sac with paired posterior lobes. Starrett

(1960) placed *baudini* in the redefined genus *Smilisca*, so indicating that call similarities are of little value in establishing the higher groupings of species.

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